5. The Life-History of the Water-Beetle *Pelobius tardus* Herbst.

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(Plates I.-III.)

Summary.

The paper has been paragraphed under the following headings:—

(1) *The Family* Pelobiidæ.

The family Pelobiidæ contains the single genus *Pelobius* and only four species, one of which is European, one Chinese, and two Australian. The family holds a somewhat isolated position, being related to the Carabidæ and showing similarities of structure with Dytiscidæ and other aquatic beetles of the series Adephaga, these being due, according to Sharp (**10**)*, not to close relationship but to adaptation to life in the water.

(2) *Britannic Distribution.*

The single European species is not uncommon in Britain, but belongs to the Southern or "English" type, as defined by Watson (**16**), being chiefly found in the Southern and Eastern counties of England. It has been recorded from one Scottish,

* The numbers refer to the bibliography at the end of the paper.

three Irish, and thirty, out of the seventy, English county and vice-county divisions.

The only Scottish record, for Midlothian, occurs in Duncan's Catalogue (**3**), where the species is described as "very scarce, Pond at Coates" on the authority of Sir P. Walker. The same record is repeated in the 'Entomologia Edinensis' (**17**), but neither Andrew Murray (**9**) nor Sharp (**11**) refers to it.

For the North of England there are two isolated records for the species, one for Northumberland South and the other for Cumberland. The former is given by Stephens (**15**) on the authority of G. Wailes: "Once near Newcastle by Mr. Hewitson." Bold's comment that this is "probably erroneous as it has never since been met with" (**4**) is quite valueless. The Cumberland record is bare, being a note by James McDougall (**8**), who mentions having taken the species at Wigton, and although I have made enquiries I can find out nothing further about it.

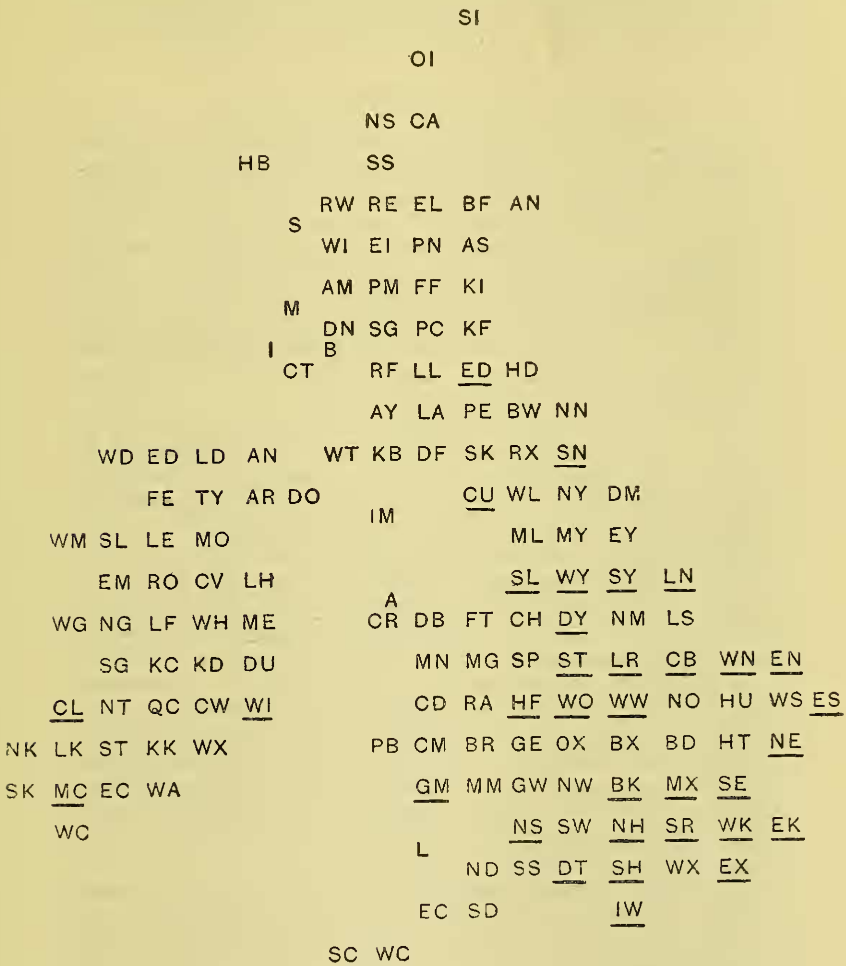
In the case of many species, records for localities far beyond the normal range are frequently regarded as due to errors in identification, but *Pelobius* is not a beetle likely to be confounded with any other, so that, unless a mistake has been made in labelling, records for this species may be regarded as correct, and are probably to be accounted for on the assumption that individuals have, from time to time, wandered northwards. In such a manner might the species extend its range, but in this case the attempts to extend northward seem to have failed up to the present.

The extreme northern range limit seems to be Yorks S.E., where the species is "fairly common in the stagnant pools near Withernsea," according to H. W. Baker of Hull (**4**). The records for Yorks S.W., Lancs S., and Derby may or may not be for single specimens in each case. The Yorks S.W. record appears in the Victoria County History (**2**) as "Doncaster (J. Wilcock)." The Lancs. record is an old one given by W. E. Sharp (**12**) as "Rufford (Gregson)," though, for some unexplained reason, this record is omitted in Sharp's later lists of 1906 (**13**) and 1908 (**14**).

The fact that Jahn (**6**) mentions "two specimens in a pool near Cheadle" seems to suggest that here again we are within the normal range of the species; and although records even south of this are scarce—in many cases only one in a county or vice-county,—there is little doubt but that the species is fairly common in the eastern and southern parts of the country. The accompanying "typo-map" will give a general idea of the distribution of the species, and the letters representing the county and vice-county names will be sufficiently intelligible, as they are more or less in correct geographical position.

Pelobius is scarcely to be described as established in Ireland, since, in the case of both Cork Mid. (**7**) and Clare (**7**), only one specimen was found, and possibly the Wicklow record, "near Lara," in the Haliday MS. (**5**) also refers to a single specimen. I have worked many of the Irish counties fairly thoroughly, and

Typomap showing Britannic distribution of *Pelobius tardus* Herbst.



Underlined letters indicate County and vice-County from which *Pelobius* has been recorded.

BK.=Berks. CB.=Cambridge. CL.=Clare. CU.=Cumberland. DT.=Dorset. DY.=Derby. ED. (Scot.)=Edinburgh. EK.=East Kent. EN.=East Norfolk. ES.=East Suffolk. EX.=East Sussex. GM.=Glamorgan. HF.=Hereford. IW.=I. of Wight. LN.=Lincoln, North. LR.=Leicester+Rutland. MC.=Mid Cork. MX.=Middlesex. NE.=North Essex. NH.=North Hants. NS. (Eng.)=North Somerset. SE.=South Essex. SH.=South Hants. SL. (Eng.)=South Lancs. SN.=South Northumberland. SR.=Surrey. ST. (Eng.)=Stafford. SY.=South-East Yorks. WI. (Ire.)=Wicklow. WK.=West Kent. WN.=West Norfolk. WO.=Worcester. WW.=Warwick. WY.=South-West Yorks.

although in some of these, *e.g.* Wexford, there were many ideal ponds, and although I was specially looking for this species, I never found a specimen. I therefore regard the Irish individuals as having strayed from the English breeding centres, the species so far having failed to establish itself west of the Irish Sea.

(3) *The Imago.* (a) *Habitat and Habits.*

Pelobius is a pond species, never, in my experience, occurring in drains, lakes, or running water, but it seems to be very particular as to the type of pond it frequents. It is apparently only found in ponds where the bottom is covered with a fine "ooze," so that gravel- or marl-pits are ideal habitats. In some cases the water of such ponds is clear and bright, while in others the pond is a favourite haunt of cattle during hot weather, the water then becoming thick and turbid and containing a high percentage of ammonia. The cattle pond is quite as thickly populated as the clean pond, so that it is the "ooze" which seems to be the important characteristic of the habitat.

In this "ooze" the beetle frequently buries itself, so that only the apex of the body, often with a protruding air-bubble, is visible, and, during the summer, it may remain thus buried for even more than thirty minutes at a time, coming up rapidly to the surface to renew its air-supply, which takes from five to ten seconds, and then once more disappearing in the mud.

By keeping the beetles in tumblers of water half filled with pond mud, I have found that at irregular intervals the air-bubble protruding from the apex of the body is released, and another then appears in its place and gradually increases in size. At first I was satisfied to explain this on the supposition that these were bubbles of exhausted air, but I can find no statement as to the mechanism of respiration in the Water-Beetle, or as to how the sub-elytral air is utilized; and I am not now inclined to speculate on the subject beyond saying that possibly the released bubbles are merely due to the expansion of the air in the sub-elytral air-space, due either to the body temperature of the insect or to the temperature or pressure of the mud.

The food of the imago consists of insect larvæ and worms, and while I was working at the life-history I kept my specimens in tumblers, feeding them mainly upon chopped-up earthworm, which they took readily. Agrionid dragonfly nymphs, *Chironomus* larvæ, *Sialis* larvæ, and various other forms, were readily devoured, but more active types, such as *Chloeon*, could usually keep out of the way.

The mouth-parts are typically mandibulate, and in nature the insect hunts for its food, swimming over the surface of the ground and poking into hollows and under stones. It seems to have a good sense of smell, since, in swimming over the surface of the mud, it will suddenly check and dive downwards; and, in such circumstances, if the beetle is dug up, it usually has some food between its jaws. Also, in my tumblers, the beetles immediately became very active when a piece of worm was quietly dropped in, even when they could not see it, and they would at once begin to hunt round until they found it.

3 (b) *Longevity of imago in artificial environment.*

In some of my tumblers I kept pairs, in others single individuals, each tumbler being supplied with a small piece of water-weed, usually *Elodea*, and also with a few pebbles to give foothold. The water was changed daily or on alternate days, according to circumstances, and I had no difficulty in keeping the beetles alive for months and even for more than a year in this way. Deaths that occurred were almost always among the pairs, and the male succumbed more frequently than the female. Presumably the cause of death in these cases was overcrowding, six or seven ounces of water, even when changed daily, not being sufficient for two individuals.

I had previously experienced this difficulty in keeping several individuals of a species in a confined space. For instance, *Hydrobius fuscipes* L., a smaller beetle than *Pelobius*, lived much longer when one was kept in each tumbler than when two or three were so kept. Of twelve individuals of such a small species as *Bidessus minutissimus* Germ. only six survived after a month, two after three months, and one shortly after that, the last survivor living for many months. At the same time six individuals of this same species, each in a separate tumbler, survived for periods varying from one to three years, the water in these tumblers never being changed, only a little being added from time to time to make up loss due to evaporation.

I have mentioned that, in the case of *Pelobius*, when one pair was confined in a tumbler the male usually died first, which suggests that the male is not so hardy as the female. Experiments showed that the female lives longer than the male. As I was unable to find the details of about a dozen experiments carried out in 1913—before the work described in this paper was commenced—I set aside four tumblers in May 1920, each containing much decaying leaf material rich in *Chironomus* larvæ and various other forms of life. In each tumbler I placed one *Pelobius*, using for the experiment two males and two females. A small piece of *Elodea* was placed in each tumbler to keep the water fresh, and each tumbler was covered with a piece of glass to reduce evaporation. Nothing was done to these tumblers until May 1921, by which time, out of the six ounces of water originally placed in each of them, only about three remained. The two females were alive but both the males were dead.

3 (c) *Stridulation.*

Pelobius used to be sold in St. Martin's Lane, London, under the name of the "Squeak beetle," owing to its being able to make a loud, strident noise, which it does by rubbing the apex of the abdomen against the underside of the apices of the elytra, in which position is a file-like structure (*vide* Pl. III. fig. 6). Both sexes are alike in this. The beetle "squeaks" when it is alarmed or annoyed; for instance, when it is caught in the water-net or held between finger and thumb. In my tumblers, if one individual tried to seize a piece of worm upon which another was feeding, the latter "squeaked," the squeak in this case presumably being equivalent to the growl of a dog with a bone.

3 (d) *Sexual differences.*

There is very little difference in outward appearance between the sexes, the larger tarsal pads of the male being about the only one. The female is slightly larger than the male on the average and perhaps slightly broader in proportion to length.

(4) *Life-history.*

The beetle is to be found in its habitat from March until October. In the latter month it descends into the mud in the bottom of the pond to hibernate, apparently remaining there without moving, its legs and antennæ folded in against the body, until the following spring. Early in March, or possibly sometimes late in February, it reappears and towards the end of March oviposition commences.

4 (a) *Oviposition.*

In the laboratory my earliest date for the appearance of eggs is March 23rd, but under natural conditions eggs are very scarce until about the second week of April, when they become common.

Whereas Dytiscid eggs are buried in the tissues of plants, the females possessing piercing ovipositors, *Pelobius* eggs are laid upon the surface of sub-aquatic vegetation. In my tumblers and tubs the eggs were laid in rows, end to end, sometimes as many as eight to ten in a row, though odd eggs were also to be found.

When about to oviposit the female lies along the plant stem, clasping it with her legs so that the apex of her abdomen touches the stem. The egg, which is blunt oval in form, 1·5 mm. long by ·87 mm. broad and equally curved at both ends, is very clear at the moment of extrusion and enclosed in a thin gelatinous envelope which at once adheres to the plant. This envelope quickly absorbs water and swells up into a thick protective covering.

Having laid an egg the beetle moves slowly forward, waving her antennæ in the water and usually touching the stem with her palpi. She moves just far enough to permit the next egg to emerge so that it will touch the end of the previous egg, and in this way she works along the stem, producing a string of eggs.

I thought at first that the beetle judged her distance by means of the palpi feeling their way, but, as I have mentioned, these organs do not invariably keep contact with the stem, while the gonapophyses do, so that it appears as if these latter decide how far forward the beetle is to move after depositing an egg.

I have not been able to determine the total number of eggs laid by a female, the greatest number of which I have a record being twenty; neither do I know whether an individual lays all her eggs during one short period or whether she lays a number of batches.

The period of oviposition for the species is a long one, lasting from March until July. I have not actually found eggs later than June 15th, but I have found very young larvæ in August under rather interesting circumstances.

On August 5th, 1915, in a disused chalk pit at Beckham in East Norfolk, where there were several shallow clear-water ponds, I found various stages of the beetle. There were old males and females, newly-emerged soft males and females, full-grown larvæ and a few larvæ not more than ten days or a fortnight old. As incubation in the warmest period of the year occupies only nine days, the eggs from which these larvæ hatched must have been laid in July.

4 (b) *Incubation.*

The earliest laid eggs took twenty-five days to hatch, but the incubation period gradually became shorter until, in June, nine or ten days became normal. Eggs laid early in April and placed in an incubator at summer temperature hatched in nine or ten days, so that temperature is evidently the controlling factor in the length of the incubation period. I shall return to this point later on.

So far as I can find, there is no special hatching apparatus such as that in the larva of *Dytiscus* (1), the shell ripping from end to end along an irregular line and apparently always along the ventral side of the embryo, however it may happen to be lying in the egg. A small pair of spines are certainly visible on the head between the eyes, near the position of the hatching spines of *Dytiscus lapponicus*, but they are not functional, as is evident from the manner in which the shell rips, and I imagine that, if anything weakens the latter along the breaking line, it must be the tarsal claws.

4 (c) *Vital Staining of the Embryo.*

In order to observe the developing embryo I removed many of the eggs from the water-plants upon which they had been laid and kept them upon cotton-wool saturated with water. I have used this method with the eggs of several other water insects—*e.g.*, Agrionid dragonflies and others, *Ranatra linearis*, and various water-beetles both Hydradephaga and Hydrophilidæ; and as a rule they do very well, but occasionally an egg shows signs of being unhealthy, that is, the surface becomes the home of numbers of minute Protozoa and Algæ. Such an egg if left to itself invariably dies, but I discovered a way of treating it which usually saved it, and this was by saturating the cotton-wool with a solution of methylene blue. Any moderate strength seemed to be suitable, and the methylene blue killed off the Protozoa or Algæ without injuring the egg. But the effect of the methylene blue was not confined to destroying the Protozoa and Algæ on the egg-shell. It did not in any way injuriously affect the developing embryo, but certain parts of the living tissues took up the stain and stood out bright blue. The staining varied with different individuals, with the same individual at different times and possibly also with different strengths of methylene blue, but in all cases the embryonic appendages of the first abdominal segment, which are well developed in this species just as they are in *Dytiscus lapponicus*, took up the stain (*v.* Pl. I. figs. 9, 10, & 11).

Otherwise the staining was very irregular. In the case of one larva just ready to hatch, the dorsal pharyngeal muscles and the malpighian tubules were stained, and on the left side of each thoracic segment and of the first two abdominal segments a short line, curved in the thoracic, straight in the abdominal segments, was also stained. At one end this line came to the surface of the embryo and suggested a spiracle, although there is no pro-thoracic spiracle in the larva and the spots were above the real meso- and meta-thoracic spiracles which were also stained. Incidentally it may be mentioned here that none of the spiracles are functional in the larva. In the abdomen of this specimen parts of the dorsal longitudinal muscle system under the terga were stained, but not evenly, certain strands having taken the stain, others not having taken it. In the alimentary canal was some greenish fluid which I took to be methylene blue changed by the action of the secretions.

I give this example merely to show the strange effect of methylene blue, and without making any attempt to explain it, I assume that the parts which stain are in some way active at the time they stain. For instance, possibly the one-sided staining of the dorsal longitudinal muscle system in the specimen referred to may have indicated that those muscle-strands were doing work while the corresponding strands upon the other side were doing none. If this suggestion is sound it might perhaps be possible, by watching any embryo develop in an egg kept in methylene blue, to recognize various parts functioning at different times.

The staining of the first abdominal appendages, which disappear after hatching, is also of some interest if this suggestion is correct. These appendages first appear when the embryo is about three days old and after the three pairs of thoracic appendages, but they are more distinct than any of the following abdominal appendages which rapidly disappear, and they persist, as more or less globular structures with a deep cup-like pit in them, right up to the time of the escape of the larva from the egg, and can be seen, especially after the staining referred to, after the larva has hatched, disappearing as it expands.

I had somewhat similar experiences as to the staining powers of methylene blue in the case of the embryos of *Dytiscus lapponicus*, and I used to run a kind of hospital of methylene-blue tumblers for the eggs. But in the case of that species I found another use for methylene blue. When rearing the larvæ I found that I could not keep them alive in tumblers, one in each, unless the water was so charged with the stain that it looked like ink, in which case the larvæ grew up quite successfully. This solution was changed every two or three days, but in no case was I successful with the larvæ in tumblers of plain water, even when I changed the water daily. Possibly the explanation in this case is that the methylene blue oxidized the fæcal products and remnants of food of the larvæ and made them innocuous.

4 (d) *The Larva.*

The larva, on hatching, is colourless and possesses a long medio-dorsal spine on the last abdominal segment and two lateral cerci. Within the egg these structures are doubled beneath the embryo, the last abdominal segments occupying the end of the egg. On escaping from the egg, the larva at once straightens out, and these appendages are at first about equal to the body-length, though before the end of the first stage the body has increased in length while the appendages remain the same.

Within an hour the chitin hardens and the pigment has appeared and darkened. The main colour of the larva is brownish green, but there is a pattern of pale yellow, and this varies in different individuals, some of which might be described as almost black with a few light markings, while others are pale yellowish with a few dark markings. The colouring apparently does not vary much during the life of the individual—that is, one which is dark in the first stage will be dark in its final stage. An infinite number of diagrams could be given to show the range from dark to light, but I have selected five specimens, two at the end of their first stage (Nos. 1 and 2) and three in their third stage (Nos. 3, 4, and 5) to show the range (*vide* Pl. I. figs. 1 to 5).

A study of these diagrams will make it clear that, although variations occur, the disappearance of the dark pigment in the lighter individuals is not a phenomenon which may happen at any spot on the surface of a segment, but occurs in more or less definite areas; and this is seen even better by comparing a number of individuals of about the same degree of darkness or lightness when a rather surprising uniformity of pattern is recognizable.

There is, I think, some very interesting work to be done upon the variations in colour-pattern within a species*. I have only paid slight attention to the subject, and only in the case of water-beetles. In many of the Hydradephaga one finds a dark ground-colour marked with yellow lines or spots, and there is usually considerable variation to be found within a species, some individuals showing more yellow and others being almost without it. Such species as *Agabus abbreviatus* F., *A. didymus* Ol., and *Platambus maculatus* L. are most interesting studies, while in such a genus as *Deronectes* four out of the five Britannic species give excellent material for research.

To return to *Pelobius*. In the newly-hatched larva the head is more or less triangular in shape and the prothorax is but little narrower than the head, the body thereafter tapering away to the last abdominal segment, which is only about one-fifth the width of the head.

The larva is heavier than water and breathes subaquatically by means of a series of filamentous gills attached at the sides of the sterna of the thoracic and first three abdominal segments. At the inside of the base of each of the front legs is a tuft of three gill-filaments. Four rather larger filaments lie inside the bases of the middle legs, and the two posterior legs have each a tuft of three gills situated as in the case of the anterior legs. The abdominal gills consist each of a pair of filaments arising from a common base, and one of these is attached on each side to the posterior edge of the sternite, those of the first abdominal segment lying posterior to the pair of embryonic appendages already referred to.

The gills are tracheate, with a single unbranched tube running the length of each filament.

The legs are long and delicate. The coxa is large, the trochanter consists of two small segments, and the femur, tibia, and tarsus are each of one segment, the tarsus bearing a pair of claws almost as long as the segment. The tarsus in each case, but more especially of the second and third pairs of legs, is strongly feathered, and therefore forms an efficient swimming organ; but it has also another function. Gilled insect nymphs and larvæ, resting in stagnant water, usually adopt some means of circulating the water about the respiratory apparatus. Agrionid dragonfly nymphs will frequently lash the abdomen from side to side; the nymphs of the Ephemerid, *Chloeon*, flap the lamellate gills ranged along the sides of the abdomen, and the larvæ of certain Perlids "dance" up and down, raising and lowering the body between the legs. The larvæ of *Pelobius* use their feathered legs as fans, the middle leg on one side and the anterior and posterior legs on the other being raised off the

* *Vide* Brown, Annetta F., "Evolution of Colour-pattern in *Lithocolletis*." Journ. Acad. Nat. Sci. Philadelphia, xvi. (1914) pp. 105–165; and Palmer, Miriam A., "Some Notes on Heredity in the Coccinellid genus *Adalia* Mulsant." Ann. Ent. Soc. America, iv. (1911) pp. 283–308.

support and rapidly vibrated so that a current of water passes under the body and bathes the gills.

The first stage of larval life occupies from six to eleven days, seven or eight days being apparently the usual period, and the larva then moults.

There is little difference in general appearance between first and second stage larvæ except that the head is more rounded and less triangular in shape, and the three "tail" processes are somewhat shorter in proportion to the body-length, but some change has taken place in the number of gill-filaments. Those of the prothorax remain as in the first stage, but there are now six filaments round the base of each of the middle legs and five round the base of each of the hind legs. The only change in the abdominal gills is the appearance of an additional pair of very small ones on the first segment, one gill towards either side of the sternite.

This stage lasts from nine to thirteen days, when the larva once more moults, reaching its third and final stage.

In the third stage again the body-length increases more than that of the "tail" processes, which are now only about one-third the body-length, and the gills are also more complex in that each filament shows several transverse constrictions, as if an attempt had been made to produce segmented filaments such as are seen in the larva of *Sialis*. As to numbers of filaments, no change takes place on the pro- or meso-thoracic segments, but an additional pair appears on the metathorax, one usually very short gill appearing anterior to and outside each of the posterior legs. The abdominal gills do not again increase in number, but remain as in the second stage. A diagram showing the arrangement of the gills will be found on Pl. III. fig. 4.

In all stages of the larva nine pairs of spiracles are to be found, two thoracic and seven abdominal, but, as has been mentioned previously, these all remain closed and functionless throughout the larval period.

As a rule it was quite easy to determine when a larva had moulted, because the cast skin would be visible in the tumbler or, if the moult had just taken place, the larva would be white, though the pigment appears very quickly after the ecdysis; but individual larvæ possessed idiosyncrasies, some always retiring into the mud just before moulting and not appearing again until their colours had been restored. I have records of quite a number of larvæ, amongst my earlier batches, which apparently grew up without moulting at all, and it was not until I discovered skins amongst the mud at the bottom of the tumblers that I realized what had happened.

4 (e) *The Food of the Larva.*

I had considerable difficulty at first in keeping the larvæ alive. I adopted the same method as that used in the case of the

Agrionid dragonfly, *Hydrobius fuscipes* and *Dytiscus*, keeping records of individuals, each in a separate tumbler, but I could find no food which they would eat. The newly-hatched *Pelobius* larva is only about 2 mm. long in body-length, so that minute food was obviously necessary, but *Paramœcium*, upon which I fed the newly-hatched dragonfly nymphs, had no attraction for them, and minute algæ, Cladocera, and Copepoda were equally useless. I noticed, when I placed a larva in a tumbler with a layer of mud at the bottom, that this mud was continually examined and even burrowed into, which suggested that the necessary food was some mud-inhabiting species. As, however, these larvæ also died, I made a journey to one of the ponds where the beetle occurred and brought home a supply of mud from there, and, on using this in the tumblers, it was at once obvious that the food-problem was solved. This mud was swarming with *Tubifex*, and it was most interesting to watch the larva hunting for and capturing its prey. It would move slowly over the surface, touching it with its antennæ and palpi, and, on discovering a *Tubifex* burrow, the larva would either at once leap into it, sometimes disappearing except for the apices of its "tails," or it would sit and watch, like a cat at a mouse-hole, its action presumably depending upon the position of the worm in the burrow. Sometimes the snatch at the prey would fail and the larva would move elsewhere, but with these first-stage larvæ it was difficult to decide whether the pounce had been successful, as it was rare for the larva to appear from the burrow with the worm in its mouth. With the larger larvæ one could see the struggle, the worm trying to withdraw to the bottom of the burrow, and the larva, as it were, sitting back upon its haunches and pulling with all its might to get the worm out. In the case of these larger larvæ, however, the feeding was sometimes done in the burrow.

The feeding process is rather peculiar; the larva sits motionless with most of the worm projecting from its mouth and wriggling furiously, the larva to all appearance doing nothing; suddenly, however, the latter makes a gulp, and a little of the projecting part of the worm disappears into the mouth. After a short interval another gulp takes place, and thus by a series of gulps the worm disappears down the "throat." The larva apparently always seizes the worm by the end, never by the middle.

So far as I could find, *Tubifex* is the only food of the larval *Pelobius*, as, although I tried various other materials and could get the larvæ to eat *Chironomus* larvæ, I never succeeded in rearing one on any diet other than the little red worm.

4 (f) *The Stomodæum of the Larva.*

The gulping down of the worm struck me as rather extraordinary. There was no chewing or biting, and yet an examination of the contents of the alimentary canal always showed chewed-up food material. An examination of the stomodæum, however, explained the mystery.

The mouth-parts consist of a pair of sharply-pointed mandibles which overlap when closed, the right overlying the left. The maxillæ are palp-like in appearance, the maxilla itself forming the basal part of the palp, and, when at rest, the whole structure is contracted by being telescoped within the base (*v.* Pl. II. figs. 1 to 4). The labium has an apical piece, which, from its appearance, I will call the "scoop" (*s*), and which, when at rest, is contracted within the basal piece which bears the two short labial palpi (*v.* Pl. II. figs. 1 to 4).

When the floor of the mouth is examined (*v.* Pl. II. fig. 1), it will be seen that at the base of the extensible part of the labium is a small, projecting piece in the median line. This piece, which I will call the "flap" (*f*), rises up in the "scoop," and when the mouth is closed this flap stands up, and the lobes of the epipharynx—this structure being split like a hair-lip—descend from above and thus block the entrance. The anterior part of the floor of the mouth is covered with minute projections arranged more or less in rows radiating from a deep groove, while the anterior part of the scoop is similarly studded. In the posterior region of the floor of the mouth is a dark brown chitinous plate (*hyp*) with a raised median piece posterior to it, and I regard these structures as representing the hypopharynx. On either side of the chitinous plate there projects inwards a membranous lobe (*mxl*) which is extremely difficult to make out; I examined a large number of specimens before I could satisfy myself that it really existed. Possibly these lobes represent the maxillulæ.

Immediately behind the hypopharynx the mouth contracts into the gullet, which is very short and opens out at once into the œsophagus (*v.* Pl. I. fig. 6). This again is very short, and there is no pro-ventriculus clearly marked off at its posterior end, but this region is armed with eight dark-coloured spines (*v.* Pl. II. figs. 5 & 6), which project forward in the walls and posteriorly are enlarged. The inner faces of these spines are armed with strong, backwardly turned teeth which are specially numerous on the enlarged bases, and evidently form the grinding-mill by means of which the food is broken up.

With the exception of a pair on each side whose bases are fused together, each spine is independent of the others. The median ventral one is the longest, and extends forwards for about two-thirds the length of the œsophagus, none of the other spines extending more than half the length of the œsophagus.

To the œsophageal walls, between the pro-ventricular spines, are attached muscles which run to the head capsule, so that the œsophagus is capable of considerable expansion and contraction. In this case, therefore, almost the whole stomodæum acts as a sucking-pump, there being no pharynx marked off for this purpose, as is usually the case.

The mechanism of all this complex apparatus seems to be as follows:—The *Pelobius* larva pounces upon the *Tubifex* and, by expanding the œsophagus, sucks the end of the worm into the stomodæum, and the mandibles then close so that the prey is held either between the two, or more usually, between the upper and the epipharynx. I think, therefore, that it usually passes into the mouth between the two lobes of the epipharynx (*v.* Pl. I. figs. 11 & 12).

At the moment of seizing upon the worm the maxillæ and labium are shot forward and the prey is received into the "scoop," and these parts then retract, the flap in the "scoop" pressing the worm upwards into the epipharyngeal slit, and the closing of the jaws bending the body of the worm upwards so that it is completely jammed and cannot move backwards or forwards (*v.* Pl. I. fig. 12). At the first suck, the end of the worm presumably reaches well down into the pro-ventricular mill, where it is well bruised, and, when this portion has been sufficiently crushed, the hold upon the worm is momentarily relaxed by the opening of the jaws and the shooting forward of the maxillæ and labium; the sucking action is repeated, and once again the mouth-parts jam the body until another section has been crushed by the pro-ventricular mill.

4 (g) *Habits of the full-grown Larva.*

The larva is full-fed about twenty-two days after the second moult, by which time it measures about 15 mm. in length, the median "tail" adding another 5 mm., and it is now ready to leave the water. In my tumblers it was always evident when this stage was reached, because the larva would swim round and round at the surface and endeavour to climb up the glass.

As I wished to watch the work of the larva in forming its pupal cell in the earth, I tried, with this species, the same method as I had used successfully with *Dytiscus lapponicus*—that is, I placed the larvæ in an earth-bottomed vivarium with a glass side, made an artificial burrow in the earth against the glass, and carefully directed the steps of the larva to the entrance of the burrow, closing the mouth of the latter when the larva had entered. With this species, however, the method did not work so successfully, as the larva, having reached the end of the artificial burrow, usually continued it on its own account and as a rule in a direction away from the glass. Digging up such larvæ and starting them again seemed to discourage them, and they were apt to sulk and make no cell at all.

I therefore devised a special glass cell consisting of two lantern-slide cover-glasses. Between these two, at adjacent corners, two small pieces of cork, half an inch thick, were placed so that, along one side, these two plates could not come into contact. Along the opposite side the two plates were brought into contact and held together by string or narrow adhesive tape. The cell was formed between these two glasses, a strip of cotton-wool filling up the open ends between the two plates and a similar strip being pushed down into the narrow angle where the two plates came together, and this cell was then filled up with sand (*v.* Pl. III. fig. 5). By keeping the cotton-wool moist by occasional wetting, the sand was also kept moist and in a suitable condition for the requirements of the larva or pupa of *Pelobius*.

An artificial burrow was then made perpendicularly downwards in the sand with a pencil, which, of course, after penetrating the sand for about 2 inches, came into contact on either side with the glass plate; and into this burrow a larva was pushed unceremoniously, the entrance to the burrow being then closed by covering the surface of the sand with a narrow strip of glass. The larva was thus in such a position that whichever way it worked it was compelled to form its cell in contact with the glass.

These glass cells were kept in the dark so that the larva should not be worried by the light, but I found that when once the larva had accepted the situation, the light did not affect it unless it was very intense.

In starting its burrow, the larva digs itself in head first, and having reached the depth at which it is going to make its cell, a depth which varies from 2 inches to at least 5 under different soil conditions, it moves its head from side to side and, with its jaws, chews up the pellets of earth, causing the grains to pack more closely, and in this way it forms a space around itself. Practically the whole space of the cell is produced by this rearrangement of the minute particles of soil, though the entrance from the tunnel becomes closed during the operation.

At first the larva, in a straight tunnel, is rather confined in its movements, but, as soon as space permits, it changes its position and sits up, alternately chewing up the pellets of soil and pressing them into the walls, using its head as a ram. The three "tail" processes, which one would expect to be very much in the way in the confined space, become very useful. They are bent over the back, like a Squirrel's tail, and wedged against the wall of the cell, and on them the body turns about freely in all directions (*v.* Pl. III. figs. 1 & 2).

The work of constructing the cell usually took from twelve to fifteen hours, though sometimes two or three days seemed to be necessary; but in these cases the larva seemed to work intermittently and without enthusiasm, whereas in most cases great energy was shown and no rest taken until the cell was completed.

After the completion of the cell the larva rests for from six to eleven days (*v.* Pl. III. fig. 3) before it changes into a white pupa of the usual Coleopterous type. The pupal period lasts about sixteen days, and the imago, white at first, takes twelve hours or longer to attain its colours, and remains in the cell for a week or more before breaking out.

(5) *The Life-Cycle.*

Thus from the hatching of the egg to the appearance of the imago occupies from nine to about fifteen weeks. On this basis, the earliest imagines should appear about the middle of June, and this raises the question whether eggs laid in July and August may not be the commencement of a second annual generation. From an examination of the ovaries of a few beetles in August which emerged in the previous June, I am inclined to think that there is normally only one generation a year. Perhaps also the longevity of the beetle, at any rate of the female, which will live for three years and perhaps longer, suggests a one-year cycle.

On the other hand, the possibility of a few precocious individuals breeding soon after emergence must not be lost sight of (and also the possibility of old females laying a second batch of eggs must be kept in mind), though it does not follow that the resulting larvæ would complete their metamorphosis.

I make this suggestion that a second generation may be commenced, even if not completed, because of a number of experiments I made some years ago with a few species of Hydrophilid beetles. By keeping these in tumblers in an incubator at a high summer temperature, 19° to 21° C. (66° to 70° F.), I found that it was possible to get egg-cocoons from some of them (e. g., *Hydrobius fuscipes* L. and *Philhydrus maritimus* Thoms.) in November, after only a month of treatment—egg-cocoons which, under normal conditions, would not have been produced until the following April or May. A hot June and July might therefore cause the ovaries of *Pelobius* to mature rapidly, and this would account for the young larvæ which I found in August at Beckham.

The life-history of *Pelobius* is interesting because of the gill-bearing larva, which does not require to come to the surface to renew its air-supply. In this respect it differs entirely from the larvæ of the Dytiscids and Hydrophilids, and resembles those of Gyrinids and Haliplids, but like, apparently, all other aquatic beetles, the pupa requires free air, and therefore, like the majority of them, the full-grown larva leaves the water and burrows into the soil, where it forms its pupal cell.

The change on the part of the larva from an aquatic to a terrestrial habit does not involve a change in the respiratory apparatus, although I had expected one or more pairs of spiracles to open during the last larval stage, as happens in the last stage of the nymph of the dragonfly. But, whereas the dragonfly nymph comes from the water into the air with the object of drying itself, the *Pelobius* larva leaves the water and quickly burrows into the earth, and therefore, presumably, is under sufficiently damp conditions to allow the gills to function until the larval skin is thrown off.

This work on the life-history of *Pelobius* was begun in 1915 as the commencement of a study of subaquatic beetle larvæ, my intention then being to work out the life-histories of a Gyrinid and an Haliplid. The work on *Pelobius* was almost completed by the autumn of that year, when military duties took me away from Cambridge.

Since my return to entomological work, time has not permitted me to continue on this line of research, and I have therefore merely completed a number of observations on *Pelobius* and written up the life-history of the beetle.

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EXPLANATION OF THE PLATES.

Plate I.

Figs. 1–5. Colour-patterns of *Pelobius* larvæ. Figs. 1 and 2 are taken from larvæ near the end of their first stage, and figs. 3, 4, and 5 from larvæ in their third stage. The specimens were merely selected to show the range of pattern, there being no noticeable difference in different stages of the same larva.

Fig. 6. Diagram of alimentary canal of a *Pelobius* larva to show proportionate lengths of Stomodæum (S), Proctodæum (P), and mid-gut (MG).

Fig. 7. The egg of *Pelobius* 24 to 36 hours old. The embryo has begun to appear. Note the large head-lobes, the first signs of the neural canal and the post. end submerged in the yolk, which, at this stage, is not segmented.

Fig. 8. The embryo about 3 days old (in June when incubation lasts only 9 or 10 days), showing the appendages appearing, the antennæ between the head-lobes and the first abdominal appendages, the last of the series at this particular stage. The yolk is now segmented and the amnion is completely formed.

Fig. 9. The embryo 4 to 5 days old (in June); the amnion still intact. The first abdominal appendages very large and distinct. The depressions at the sides of the thorax and first abdominal segments are, presumably, the commencements of tracheal-tube formation, though the fact that there is no prothoracic spiracle perhaps makes this doubtful.

Fig. 10. The embryo 7 or 8 days old (in June). The eyes have just developed, the membranes have ruptured, rolled back, and disappeared within the dorsal region of the embryo. The first abdominal appendages are now smaller.

Fig. 11. Front view of head of a third-stage larva to show the relative positions of parts. CL=Clypeus. LBR=the labral ridge, beneath which are the two epipharyngeal lobes, EP. F is the "flap" standing up in the "scoop" of the labium, LAB. LAB.P=labial palp. Mx=maxilla, sunk in its base. Mx.P=Maxillary palp. M=Mentum. GU=Gular sclerite of head capsule. ANT=Antenna. O=Ocelli. MDB=Mandibles which are in a position for seizing the prey.

Fig. 12. Front view of head as in fig. 11, except that a worm is in the mouth and the mandibles have closed upon it. This diagram shows how the worm is bent upwards by the mandibles and thus jammed so that it cannot move backwards or forwards.

Plate II.

Fig. 1. Mouth-parts of a third-stage larva with labrum, epipharynx, and "roof" of mouth removed to show the relative positions of labium (LAB), maxilla (Mx), fully extended, and mandibles (Mdb). S=the "scoop" fully extended and F, the "flap" in the "scoop." Mxl possibly represents the maxillulæ. Hyp, a dark chitinous plate in the floor of the mouth just where it narrows to the "gullet," presumably represents the hypopharynx. Note the four holes in this plate which seem to be always present.

Fig. 2. Labium and maxillæ as in fig. 1, but with the "scoop" fully retracted and the maxillæ almost fully retracted within their bases.

Fig. 3. Ventral view of labium and maxillæ, showing the "scoop" fully extended and one maxilla extended and the other fully retracted within its base. M=mentum, not clearly marked off from the bases of the maxillæ, but recognizable. G=the gular sclerite.

Fig. 4. Ventral view of labium as before, but with the scoop fully retracted. It will be seen therefore that the scoop *telescopes* into the rest of the labium just as the maxillæ do into their bases.

Figs. 5 & 6. Views of the pro-ventricular spines of a third-stage larva, *in situ*, showing the backwardly directed "teeth" and hairs on the inner faces. Fig. 5 is a view from above and fig. 6 is a lateral view. These two figures are from camera lucida drawings, and the millimetre scale indicates their magnification.

PLATE III.

Figs. 1 & 2 are from sketches of the positions adopted by the larva at work when constructing its cell.

Fig. 3 shows the position of the larva resting in the completed cell, waiting to change into a pupa.

Fig. 4. Ventral view of a third-stage larva, showing the gills on the left side of the thoracic and right side of the abdominal segments, the others having been omitted for the sake of clearness. This diagram is based upon a camera lucida drawing, Cc=Coxal cavity. Sp=the closed meso- and meta-thoracic spiracles.

Fig. 5. A diagram of one of the glass cells used to enable the work of cell construction by the larva to be watched.

Fig. 6. Under side of the right elytron of a male specimen of the beetle to show the file, upon which the apex of the abdomen rubs to produce the "squeak." There is a file on each elytron, and the files are alike in the two sexes.